Studies on the Taxonomy and Ecology of Planktonic Rotatoria

by

BIRGER PEJLER

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ALMQVIST & WIKSELLS BOKTRYCKERI AB

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THESIS

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BY

BIRGER PEJLER
FIL. LIC., SÖDERM.

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The thesis is a summary of the following papers published by the author:

I. Introgression in planktonic Rotatoria with some points of view on its causes and conceivable results. *Evolution, 10,* pp. 246–261. 1956.

II. On variation and evolution in planktonic Rotatoria. *Zool. Bidr. Uppsala, 32,* pp. 1–66. 1957.

III. Taxonomical and ecological studies on planktonic Rotatoria from northern Swedish Lapland. *K. svenska VetenskAkad. Handl.*, ser. 4, vol. 6, No. 5. 68 pp. 1957.

IV. Taxonomical and ecological studies on planktonic Rotatoria from Central Sweden. *K. svenska Vetensk.-Akad. Handl.*, ser. 4, vol. 6, No. 7. 52 pp. 1957.

In the following these papers will be referred to by the above Roman figures.

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Material and Methods

The investigation is based upon material from northern Swedish Lapland and from the provinces Uppland and Närke in Central Sweden. Lakes as well as smaller waters (tarns, ponds, pools, etc.) have been visited. Some waters have been examined during all seasons, others only in summer. In Lapland quantitative samples have been collected to a large extent, whereas only qualitative samples have been taken in Central Sweden. Also in the latter case the author has attempted the estimation of the frequency which has been indicated by 1, 2, or 3 crosses. For the quantitative methods and for the establishment of the frequency diagrams the reader is referred to III, p. 6.

Faunology and Ecology (III, IV)

A greater number of planktonic Rotatoria has been encountered in Central Sweden than in Lapland (60 and 39, respectively) in spite of the fact that the latter area is the one which has been most thoroughly studied. The main reason for this is scarcely to be sought in a larger average number of species in the waters of Central Sweden, taken individually, as compared with the richest waters of Lapland: 21 planktonic rotifers have been established in the lakes Nedre Laksjön and Rakkurijärvi, both in Lapland. This figure is surpassed only in two of the localities in Central Sweden, viz. the eutrophic lakes Erken and Valloxen, in which 24 and 22 species, respectively, have been observed. (The large lake Mälaren with its many bays of highly varying nature is disregarded in this connection.)

The reason for the above-mentioned regional difference in the wealth of species has to be looked for rather in the circumstance that in Central Sweden the different types of waters exhibit much greater differences in the composition of the fauna than in Lapland. Whereas in Lapland all the more common planktonic rotifers of the lakes (with the exception of *Filinia terminalis*) occur likewise in the smaller waters, several of them are absent in the ponds and pools of Central Sweden. These contain species of their own instead, different in different types of waters (duck ponds, peat pits, etc.), and which are usually absent in the material from Lapland.

Between different types of lakes also, the composition of the fauna of rotifers exhibits fairly great differences in Central Sweden. A number of special forms particularly characterize the plankton of the eutrophic lakes. In Lapland, on the contrary, lakes at the same altitude contain a relatively similar plankton of rotifers. The number of species decreases on the whole with rising altitude. The highest-situated lakes (and tarns) contain only some few euryecious species in so far as they harbour any planktonic rotifers at all. Special alpine or arctic species are absent.

Particularly rich in species seem to be those lakes which are tolerably rich in nutrition, but not strongly influenced by civilization, and which are in addition deep enough and sufficiently warmed up during the summer to develop a stable temperature stratification. The number of species decreases on the whole with (1) increasing altitude (in the case of the area of examination in Lapland, where the waters lie between 345 m and about 1 300 m above sea-level), (2) decreasing size of the water, (3) increasing inflow and outflow, and (4) decreasing autotrophy. Everything seems, however, to indicate that for optimal conditions autotrophy must not exceed a certain value. The number of species is at all events relatively low at times of strong water-bloom due to blue-green algae. (Such water-bloom has been established in connection with considerable pollution.)

The ecology of different species has been shown to be correlated with the following environmental factors: (1) temperature, (2) light, (3) content of oxygen, and (4) trophic level. Certain species are limited mainly or exclusively to strongly dystrophic waters, others to small waters (members of the last-named category being found occasionally in the vegetational belt of the lakes).

Competition between different species is avoided in different ways, as (1) by different demands on temperature, (2) by a different ability to survive in water poor in oxygen, (3) by a higher or lower degree of specialization to the plankton habitat proper (some species seem to live preponderantly in the "edge zone" between the periphytic-benthic and the planktonic environments), (4) by occurrence in waters belonging to different types (with regard to trophic level, content of humus, size, etc.; see above), and (5) by nutritional specialization.

Morphological Variation (II)

Within the individual waters the intraspecific variation is occasionally rather considerable. Its course is as a rule more or less continuous. In some cases, however, a distinct discontinuity in the variation has been shown within individual waters without, in the author's opinion, justi-

fying the distinction of several species (in *Keratella cochlearis* and *Notholca labis*).

Considerable differences with regard to morphology often exist also *between* the different populations within the respective areas examined by the author. Similar to the variation within the populations it seems as a rule to follow a continuous course, and ecoclines have occasionally been established. In exceptional cases it is possible to speak about a discontinuity inasmuch as some populations without any particularly distinctive environmental conditions diverge more or less strongly from the other populations. In these cases it is the question of relatively small populations, and also other circumstances seem to indicate that the morphological divergences in question have originated from "genetic drift".

The author's material is derived from three comparatively small geographical regions, and therefore in itself hardly allows any conclusions about geographical variation in the proper sense of the term. Comparison with the statements in the literature occasionally permits, however, the detection of indications of such variation (as in *Notholca labis*). So far it seems as a rule impossible to decide, whether or not this variation follows a continuous course, and to what extent it permits the distinction of subspecies.

It appears extremely probable that the intraspecific morphological differences mentioned often rest upon a genotypical basis, and in certain cases arguments in favour of this assumption have been supplied. Factors which contribute to the intensification of the morphological variation between the populations are (1) the more or less pronounced spot-distribution characteristic of all fresh-water organisms, especially those living in stagnant water, (2) the occurrence of obligatory or (usually) facultative parthenogenesis, and (3) introgressive hybridization. A great ability to disperse, on the other hand, counteracts the local morphological variation.

Introgressive Hybridization (I, II)

Forms which have been interpreted as introgressive have been encountered within the genera *Conochilus* (in Lapland) and *Polyarthra* (in Lapland and Central Sweden). In Central Sweden introgressive forms of *Polyarthra* have been mainly met with in biotopes under the influence of civilization (in small, artificial ponds), and on this point their occurrence agrees with that of the majority of introgressive forms observed in the plant kingdom. In Lapland, on the other hand, the introgressive forms live in natural accumulations of water, but the environment seems

in all cases to offer relatively few niches for planktonic rotifers, since these are represented by only a small number of species. Closely related species have never been found simultaneously in such extreme environments. This fact might be explained by the assumption that their ecological niches have become fused. Such a "collective niche" can be peopled by one of the two species which have had their niches fused. Frequently, however, introgressive forms which combine the characters of the two species in question ought to be best adapted for the collective niche. By reason of their high heterozygosity introgressive forms exhibit furthermore a relatively wide variation, and can be expected on this account to fill the vacant niche in a more efficient way than either of the parent species could do. On the basis of the points of view mentioned it is not surprising that the introgressive forms, found in Lapland, live on the whole in environments which are more extreme than those of the parent species. Frequently the introgressive forms occur in waters from which both parent species are missing. We can thus talk here about a low degree of geographical (or rather topographical) isolation from the parent species. It appears not improbable that such introgressive forms can develop occasionally in such a direction that they come to constitute new species side by side with their parent species if they come into new localities which are rich in niches.

Introgressive hybridization is probably much more widely spread among the planktonic rotifers than what appears from the above, but in other cases its detection may for different reasons be rather difficult. Also in cases other than those referred to above morphological deviations have been discovered of such a kind that introgression of closely related species can be suspected. The discontinuous variation in *Keratella cochlearis* and *Notholca labis* in some individual waters can be thought to depend on the original presence of two or more species which have now become fused by hybridization in the majority of localities (at least in the respective areas examined by the author), but which in localities particularly rich in niches or especially original (not influenced by man, etc.) are still isolated from each other. In this particular case, however, this may not be the only possible explanation.

Taxonomy

The authors studies of the local variation have demonstrated the appropriateness of certain changes in the taxonomy. Thus *Filinia limnetica* has been incorporated with *F. longiseta* (II), *Filinia maior* with *F. terminalis* (II, III), and *Notholca limnetica* with *N. labis* (II). The species *Conochilus norvegicus* can no longer be maintained (I, III).

Two forms among the material from Central Sweden, viz. *Pompholyx triloba* and *Synchaeta wesenberg-lundi*, deserved in the authors opinion to be treated as new species (IV).

Males and Sexual Periods (mainly III)

The males of *Kellicottia longispina* and *Collotheca libera* are described. The resting egg of *Anuraeopsis fissa* and a new type of egg (probably a resting egg) of *Synchaeta pectinata* are figured.

The investigation in Lapland in particular has yielded a fair amount of material referring to the times for the setting-in of the sexual periods in the different species. In the cold stenothermal species resting eggs are formed mainly at the time of the débâcle (or immediately afterwards), in the warm stenothermal species during late summer and autumn, in the eurythermal forms during late summer, autumn or early winter. Sexual periods have practically never been observed in waters with small seasonal changes of environment (alpine waters, Torneträsk).

Micro- and Macroevolution (II)

The development of new species seems as a rule to be linked with geographical isolation. At least within the order Bdelloidea, which includes almost exclusively non-planktonic species, the development of new species takes place under continuous reproductive isolation (depending on obligatory parthenogenesis).

Closely related species can be isolated in different ways, geographically, ecologically, and by parthenogenesis. Of ecological isolation both isolation of habitat and seasonal isolation have been established. The species are able to avoid competition for food by geographical or ecological vicarious distribution. More common, however, seems to be the case of sibling species wich exhibit a distinct difference in size that finds its counterpart in the food particles.

Certain circumstances indicate that occasionally a formation of species occurs which takes place entirely within the plankton habitat. The planktonic species seem on the other hand rarely or never to have formed points of junction on the phylogenetic main roads. They seem rather to represent isolated branches or terminations of branches, situated here and there upon the ancestral tree of the Rotatoria.

Almost all planktonic rotifers exhibit morphological structures which can be supposed to increase buoyancy. The development of these structures can be assumed to have taken place gradually and often in connec-

tion with a change of function. Several examples have been outlined for the way in which such an evolution might conceivably take place. On the transition to a planktonic mode of life the foot and the foot glands usually are either reduced or change their function.

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